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Fish stock development in the Central Baltic Sea (1974–1999) in relation to variability in the environment

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Cod, sprat, and herring are the commercially most important fish species in the Central Baltic Sea. In the present study, dynamics of stock abundance and biomass of these species were reconstructed using Multispecies Virtual Population Analysis. The cod stock declined from an historic high during the early 1980s to its lowest level on record at the beginning of the 1990s, showing no sign of recovery afterwards. The sprat stock size increased to a historic high level concurrently, while herring abundance was slightly reduced. However, a substantial reduction in herring weight at age resulted in a continuous decline of the total biomass from the early 1980s. A review of recruitment processes influenced by the variable physical environment was performed for cod and sprat, i.e. the species most intensively studied and showing the largest variability in stock sizes. The most important processes are (i) egg production in dependence of ambient hydrographic conditions and food availability, (ii) egg developmental success in relation to oxygen concentration and temperature at depths of incubation, (iii) egg predation by clupeids dependent on predator–prey overlap, (iv) larval development in relation to hydrographic processes and food availability, and (v) predation on juveniles. All the above processes negatively affected the cod population, while the sprat stock benefited from them, despite a developing industrial fishery, resulting in a regime shift from a cod to a sprat dominated system in the Central Baltic.

Keywords: Baltic Sea, environmental variability, fish stock development, regime shift, reproductive success, species interaction.

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Introduction

The Baltic Sea is characterized by large horizontal and vertical hydrographic gradients which have significant influence on the spatial distribution and regional community structure of the fish species as well as their zooplankton and benthic prey (Arndt, 1989). As is typical for estuaries, marine and freshwater organisms are found in a regional succession with species-specific ranges of distribution. Depending on their preferences and tolerances for salinity, oxygen, and temperature, most species in the Baltic

approach the limits of their general distribution. Hence, they show an increased vulnerability and stock size variability related to changes in the environment which potentially affect the fishery.

The fish community in the open sea areas of the Baltic can be characterized by three dominant species, i.e. cod (*Gadus morhua callarias* L.), sprat (*Sprattus sprattus* L.), and herring (*Clupea harengus menbras* L.), sustaining more than 95% of the commercial catch (Sparholt, 1994). Throughout the past two decades, the cod stock declined from an historic high (early 1980s) to its lowest level on record (beginning of the 1990s), hardly recovering afterwards (ICES, 2001a). This stock development was caused by a combination of recruitment failure and high fishing intensity (Bagge *et al.*, 1994). The decline of this top predator in the system resulted in a release in predation pressure on sprat (Sparholt, 1994), and in combination with high reproductive success and relatively low fishing mortalities caused a pronounced increase in sprat stock size (Parmanne *et al.*, 1994; Köster *et al.*, 2001a). Both cod and sprat aggregate in deep Baltic basins to spawn, and historically their spawning times overlap (Bagge *et al.*, 1994; Parmanne *et al.*, 1994). Nevertheless, their reproductive success appears to be out of phase and largely independent of their spawning stock size, suggesting that environmental processes significantly affect recruitment success (e.g. Köster *et al.*, 2002). The population development of the other abundant clupeid species in the Baltic, herring, seems to be more stable and independent of the cod stock, because only juvenile herring are preyed upon intensively by cod (Parmanne *et al.*, 1994).

In the present study, we reconstructed the stock abundance and biomass of cod, sprat, and herring in the Central Baltic Sea using Multispecies Virtual Population Analysis (MSVPA). Further, we reviewed recruitment processes, especially those possibly influenced by the variable physical environment. In this review, we concentrated on cod and sprat as both species show high contrast in stock development and detailed information on processes affecting their reproductive success has accumulated throughout the 1990s.

Although not all processes are completely understood and quantified yet, they explain most recent cod and sprat stock trends. Based on this information, we describe how these processes resulted in a regime shift from a cod to a sprat-dominated system in the Central Baltic.

As fisheries also have a pronounced impact on the population dynamics of both species, information on the development of the fishing intensity is given. However, the present study does not intend to give a comprehensive overview of interrelationships between hydrographic conditions, fisheries actions, and ultimately stock dynamics, although this is a potentially rewarding research area.

Material and methods

The MSVPA incorporates cod as the top predator in the system and cod, sprat, and herring as prey (Sparholt, 1994). This allows quantification of predation on juveniles and the determination of pre-recruit abundance not available from standard assessment (ICES, 2001a; Köster *et al.*, 2001a).

The stock units utilized in the present MSVPA for the Central Baltic are: cod and herring in ICES Subdivisions 25–29 and 32 and sprat in Subdivisions 25–32 (Figure 1). As the sprat population in Subdivisions 30 and 31 is extremely low (ICES, 1999a), the MSVPA derived stock estimates refer in principal also to Subdivisions 25–29 and 32.

In the present analysis, the stocks are composed of age groups 0 to 7+ for cod, 0 to 9+ for herring, and 0 to 7 for sprat, with the + indicating the oldest category included – age 7 and older for cod and age 9 and older for herring. Quarterly catch-at-age in numbers and weight-at-age in the catch were revised by ICES (1999a) for the years 1977–1997 and updated for the period 1976 and 1998–2000 by ICES (2001a). Weight-at-age in the catch was assumed to be equal to the weight-at-age in the stock, exceptions being age groups 0 to 2 for cod. Here, because of size selection by commercial gears, period-specific (before 1989 and after 1990) average weights derived from trawl surveys and compiled by ICES (1999a) were applied.

To identify the spawning component of the cod stock, existing maturity estimates were employed as averages over the periods 1980–1984 (applied also before 1980), 1985–1989, and 1990–1994, year-specific data for 1995–1997 for combined sexes as presented in ICES (1999a), updated with data for 1998 and 1999 according to ICES (1999b and 2000). For 2000 an average over the years 1997–1999 was utilized. Maturity ogives of sprat and herring were used as given in ICES (1996), being constant over time and areas.

Quarterly relative diet compositions and individual food rations are based on cod stomach content data covering the period 1977–1993 according to Subdivision (ICES, 1997a). The Subdivision-specific data were averaged applying relative distribution patterns obtained from trawl surveys as spatial weights (ICES, 1997a) kept constant for 1996–2000. The quarterly consumption rates were revised based on re-calculated ambient temperatures (ICES, 2001b) according to the procedure outlined by ICES (1999a). The consumption model in use corresponds to the model applied in the North Sea (ICES, 1997b), based on a general model of gastric evacuation, considering actual environmental temperatures and predator weights as additional variables (Temming and Herrmann, 2002). As stomach content data are available for most of the quarters

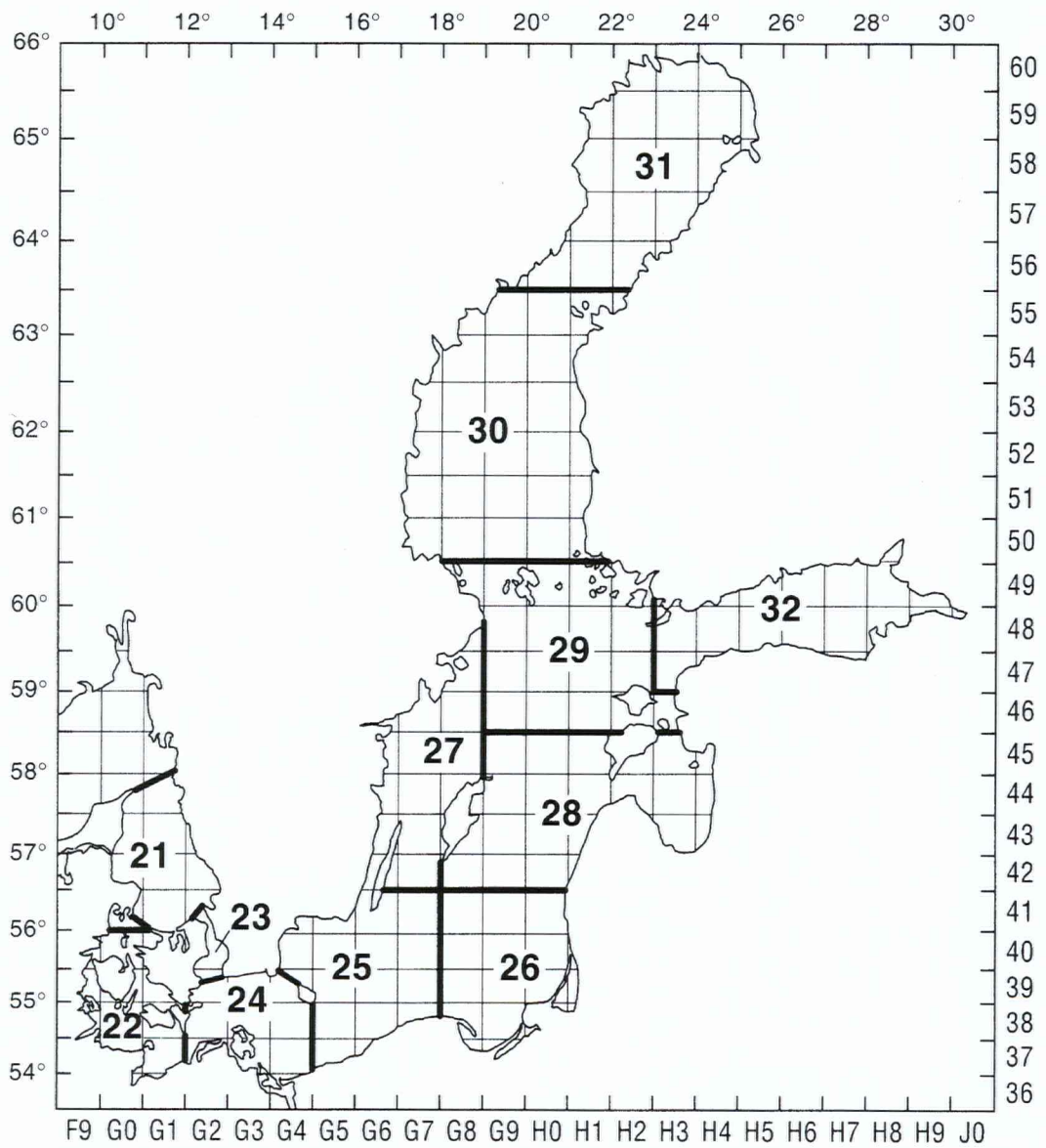

Figure 1. Study area of the Baltic with ICES Subdivisions (numbers).

and years covered by the present MSVPA, consumption rates were computed for every predator age group, quarter, and year. Missing quarters/years, i.e. also the years 1976–1977 and 1994–2000 were predicted by a multiple linear regression model with Subdivision, year, and predator weight as independent variables (ICES, 1999a).

The residual natural mortality rate was assumed to be 0.2 per year for all three species, equally distributed over quarters, corresponding to standard MSVPA runs in the Baltic (Sparholt, 1991). Suitability coefficients of prey species age groups as food of specific predator age groups (Sparre, 1991) were estimated according to the standard suitability sub-model implemented in the Baltic MSVPA, with the biomass of other food set constant over time, corresponding to earlier MSVPA runs (ICES, 1997a).

The tuning of the MSVPAs was performed with the new 4M-programme routine iteratively running XSAs (Extended Survivor Analysis) and MSVPAs (Vinther, 2001). Abundance indices utilized for tuning originated from the international bottom trawl survey directed to cod, performed annually in February/March (Sparholt and Tomkiewicz, 2000) and the international hydroacoustic survey directed to herring and sprat, conducted in September/October (ICES, 2001a). XSA settings were identical to those used in the standard assessment (ICES, 2001a). Fishing mortalities in the terminal year for

the 0-groups and for 1-group cod were not estimated in the XSA tuning, and values were tuned to reach abundances close to the average values estimated in period 1995 to 1999.

Results

Stock abundance

The stock abundance of cod in the Central Baltic is characterized by a pronounced increase from 1976 to 1980, remaining high until 1983, afterwards steadily declining to its lowest level on record in 1991, and since then has been close to the historic minimum (Figure 2). The estimated stock size of sprat shows a reverse trend, with a decline from 1975 to 1980, low levels until 1988, followed by a pronounced increase to the highest stock size on record in 1996 and a decline in most recent years. In contrast, the herring stock appears to be fairly stable, with deviations of less than 25% around the long-term mean and a slight downward trend in most recent years.

Spawning stock biomass

Spawning stock biomass (SSB) of cod and sprat follow similar time trends as the abundance; however, some deviations are apparent (Figures 3A, B). Cod SSB remained longer on a high level until 1985 and recovered to a certain degree after the minimum in early 1990s, which is barely noticeable from abundance estimates. Sprat SSB declined by 26% from 1997 to 1999 (Figure 3B), while abundance showed a more pronounced decline by nearly 40%. In contrast, SSB of herring declined by around 50% from the early 1980s (Figure 3C), a trend which is far less pronounced in stock abundance.

Recruitment

Examining the effect of the spawning stock on recruitment revealed a high reproductive success in cod at intermediate SSB values in the 1970s and declining reproductive success at historically high spawning stocks from 1981 to 1985 (Figure 3A). Sprat recruitment showed a positive development from the mid-1980s to the mid-1990s, with high fluctuations in most recent years, virtually independent of the SSB (Figure 3B). For herring, an overall trend of declining recruitment with declining SSB is indicated, however, with considerable inter-annual variability (Figure 3C).

Weight-at-age

Concurrent with the decline in stock size of cod, there was an increase in weight-at-age 3 and older

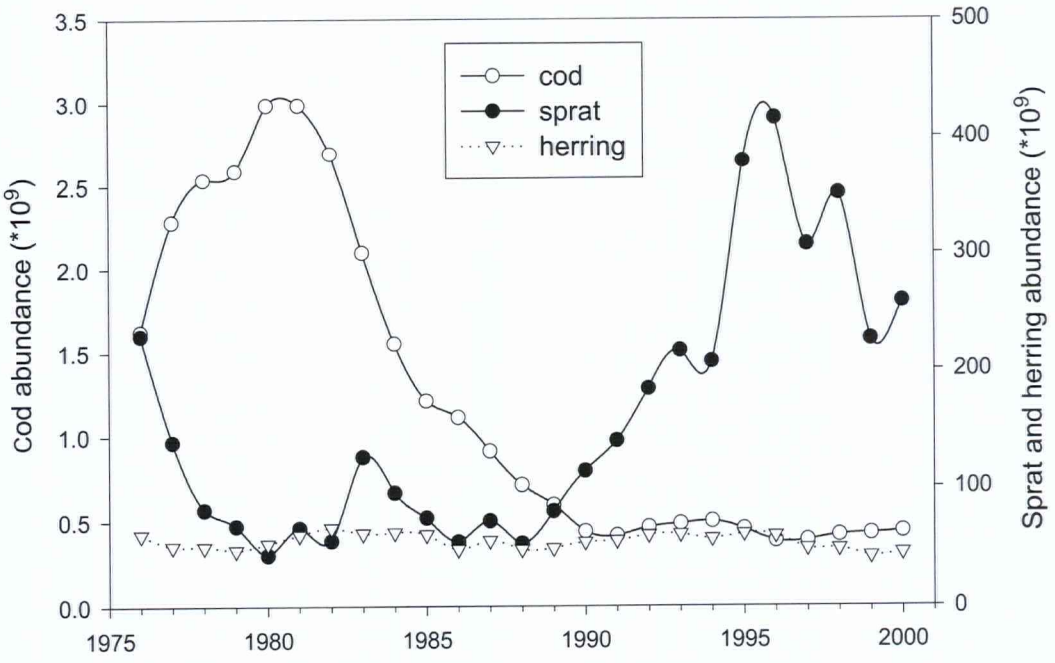

Figure 2. Population sizes of cod, sprat, and herring (age group 1 and older, beginning of the year) in the Central Baltic.

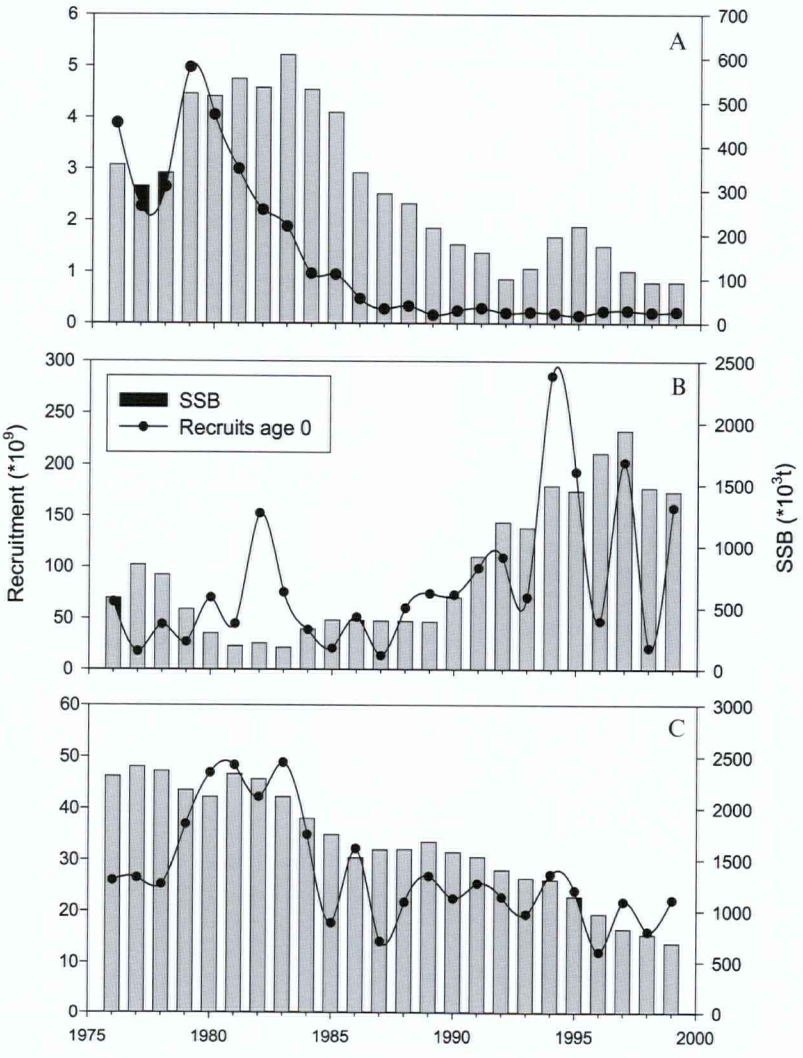

Figure 3. Spawning stock biomass (SSB) (2nd quarter) and recruitment (age group 0) of cod (A), sprat (B), and herring (C) in the Central Baltic.

(Figure 4A). Average weight-at-age of sprat showed a substantial decline from 1990 to 1997 and a reverse trend in most recent years (Figure 4B) also concurrent with the opposite trend in stock abundance. Independent of stock size, the weight-at-age of herring declined from 1983 to 1996 by more than 50% (Figure 4C).

Predation mortality

A pronounced time trend in the estimated mortality of cod through cannibalism is apparent (Figure 5A), with increasing predation mortalities until 1983 and a decline until 1991, being stable and low afterwards. Age-specific differences in predation mortality are obvious, with cannibalism rates on 0-group being considerably higher (instantaneous mortality due to predation reaching maximum values >1.0) than on 1-group cod (maximum 0.61), especially when considering that the mortality rates on 0-group refer only to a half-year period. Predation on 2-group cod was in general low, i.e. less than 50% of the applied residual mortality of 0.2. 0-group sprat do not suffer from high predation pressure, while age-group 1 (maximum around 1.1) and also, to a lesser degree, adult sprat do (maximum 0.51). Intense predation pressure on sprat occurred in 1979–1983, with a subsequent decrease until 1991 driven by the decline in predator population size (Figure 5B). The time trend in predation mortality of herring is similar to that of sprat; however, the absolute values are lower for age-group 1 (in maximum 0.66) and especially for adult herring (in maximum 0.17), while 0-group mortality rates are similar in both species (Figure 5C).

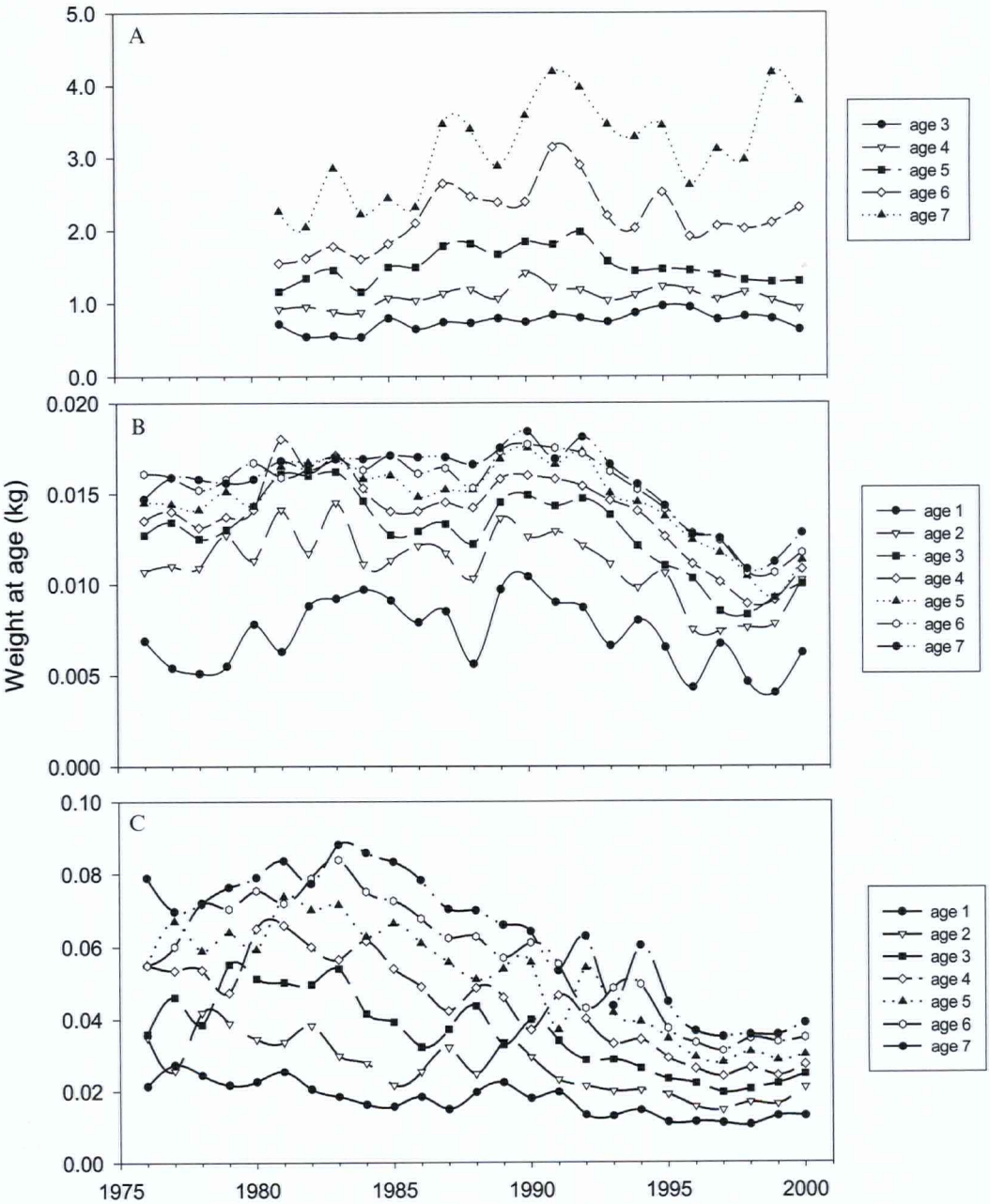

Figure 4. Average weight-at-age (beginning of the year) of cod (A), sprat (B), and herring (C) in the Central Baltic.

Fishing mortality

The average fishing mortality of cod age groups 4–7 increased from 0.4 in 1979 to 1.4 in 1991 and decreased sharply to the lowest level on record in the following two years (Figure 6A). This reduction is caused by rigid enforcement of management measures, i.e. a TAC reduction for the entire Baltic from 171×10^3 t in 1991 to 100×10^3 t in 1992 and 40×10^3 t in 1993. Afterwards, a pronounced increase in fishing mortalities to the original high level is indicated due to increasing fishing effort (ICES, 1998) at declining stock size. The fishing mortality of sprat and herring were substantially lower throughout the entire time period, i.e. ranging from 0.09 to 0.48 with an increasing trend since the early 1990s.

The corresponding yield to biomass ratios followed in general the development of the fishing mortality, with a less steep decline for cod at the beginning of the 1990s (Figure 6B). On average, 41% of the cod biomass available at the beginning of the year was removed by the fishery, ranging between 22% in 1978 and 64% in 1991. In sprat and

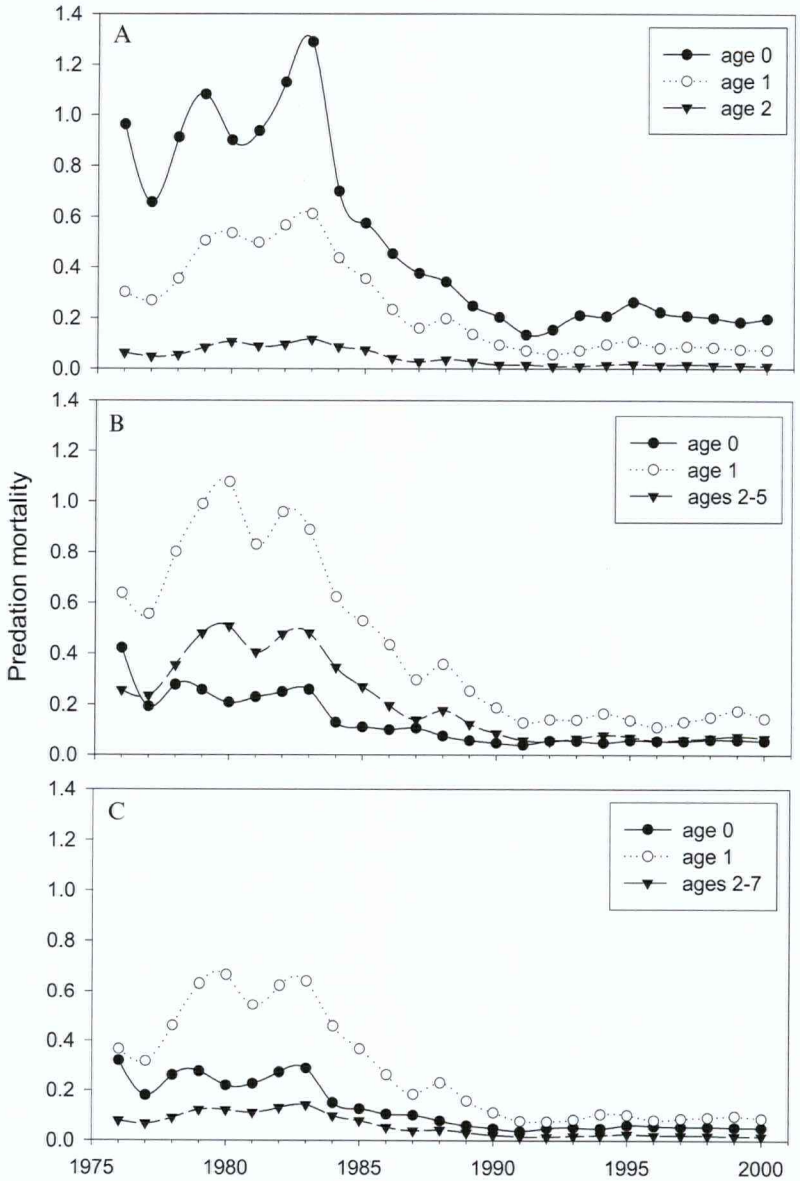

Figure 5. Annual predation mortality rates of cod age group 0, 1, and 2 (A), sprat age group 0, 1, and 2–5 (B), herring 0, 1, and 2–7 (C) in the Central Baltic. Note predation mortality of 0-group refers to 3rd and 4th quarters.

herring the corresponding removals are on average 11% and 16%, respectively, with higher variability in sprat.

Discussion

Validation of stock trends

Stock development trends derived by the multispecies and the standard stock assessment (ICES, 2001a) are similar, with the MSVPA additionally covering younger age groups (i.e. age group 0 and for cod also age group 1). Revision of the quarterly consumption rates of cod did not change this feature. The reconstructed stock abundances are furthermore in accordance with trawl and hydroacoustic surveys utilized for tuning of the MSVPA (Vinther, 2001). Deviations between time trends in stock abundance and spawning stock biomass can be explained in all three species by changes in weight-at-age, and in cod additionally by an earlier maturation in the 1990s compared to the 1980s (Tomkiewicz *et al.*, 1997).

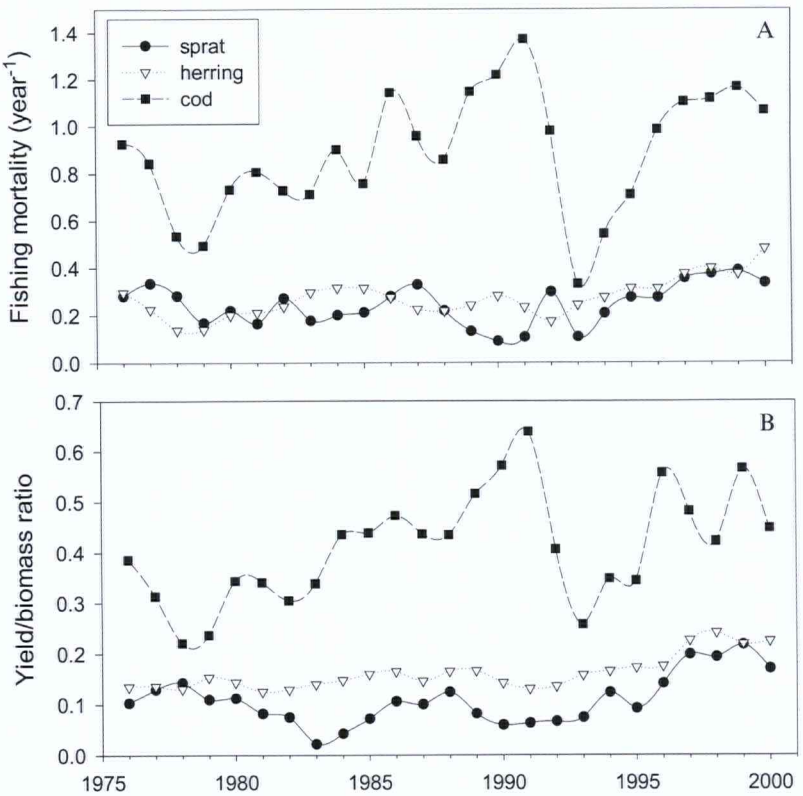

Figure 6. Annual average fishing mortality rates of sprat and herring age groups 3–5 and cod age groups 4–7 (A) and yield per biomass ratio of the three species in the Central Baltic (B).

Egg production

Timing and duration of spawning is potentially an important source of variability in the reproductive success of Baltic fish stocks owing to seasonal changes in: (i) environmental parameters (MacKenzie *et al.*, 1996), (ii) spatial overlap of early life stages with predators (Köster and Möllmann, 2000a), and (iii) transport of larvae into areas with sufficient food supply (Hinrichsen *et al.*, 2001 and 2002a). Duration of the spawning activity of the cod stock depends on its size structure and sex composition; however, the timing of peak spawning is hardly affected by these factors (Tomkiewicz and Köster, 1999). Consequently, the observed shift in the main spawning time of cod from May/June to July/August at the beginning of the 1990s is likely to be caused by other processes as well (Wieland *et al.*, 2000). Potential candidates include removal of early spawners by the fishery, which is mainly directed to pre-spawning and early spawning concentrations (ICES, 1999b) and a coupling to ambient temperature (Wieland *et al.*, 2000).

Age-specific sex ratios and maturity ogives of cod derived from the International Baltic Trawl Survey (Tomkiewicz *et al.*, 1997; STORE, 2001) showed: (i) a dominance of females with increasing age, (ii) that males generally mature at a younger age than females, (iii) that the age at which sexual maturation occurs increases with distance from the Kattegat and the Danish Straits, as the transition area between the North Sea and the Baltic, and (iv) that maturity-at-age shows significant variability between different time periods. Thus, the quantity of the egg production of Baltic cod depends on the age structure of the stock, as well as the location and time period. Variability in maturation appears to be coupled to growth rates, reflected in decreasing age at sexual maturity concurrent with increasing weight-at-age (STORE, 2001).

An analysis of individual Baltic cod fecundity revealed that the relative fecundity, i.e. the total number of developing oocytes per unit of body weight, is independent of body size (Kraus *et al.*, 2000). Relative fecundity varied significantly between years, but not between spawning areas nor between different months within one spawning season (Kraus *et al.*, 2000). On an individual level, a weak impact of the nutritional status of the female on the relative fecundity was detected, while on a population level a clear dependence on food availability has been shown (Kraus *et al.*, 2002). Inclusion of temperature improved the relationship further, but overall had a limited influence on

relative fecundity. In conclusion, an increase in weight-at-age, a decline in size/age of attaining maturity and an increasing individual fecundity with decreasing stock size and increasing prey availability has had a compensating effect on the total egg production by the stock.

In Baltic cod a significant relationship exists between the potential egg production by the spawning stock and the realized egg production as determined from egg surveys (Köster *et al.*, 2002). Apart from problems in parametrization of each of the input data series, remaining variability may be related to (i) atresia, i.e. resorption of oocytes before spawning, due to unfavourable environmental conditions during spawning, as demonstrated for Atlantic cod (Kjesbu *et al.*, 1991), (ii) variable fertilization success in relation to salinity changes (Westin and Nissling, 1991), and (iii) differences in egg mortality already in the first developmental stage.

A number of investigations on different species, including cod, suggest that egg and larval viability is positively related to egg size (see Trippel *et al.* (1997) for review), and that egg size varies according to female age/size and condition as well as spawning experience. For Baltic cod, significant positive relationships between (i) egg size and female size, (ii) egg size and larval size/growth, (iii) egg size and survival during the yolk sac stage, and (iv) egg size and egg buoyancy, have been established (Nissling *et al.*, 1998; Vallin and Nissling, 2000). This implies higher egg and larval survival for offspring originating from large females, especially as larger and more buoyant eggs have a higher chance of avoiding oxygen-depleted bottom water layers. Consequently, the reduction in the share of older females in the spawning stock from the mid-1980s to the early 1990s (Wieland *et al.*, 2000), caused by heavy fishing pressure, has had a negative effect on the reproductive success of the Central Baltic cod stock (Vallin and Nissling, 2000).

The temporal pattern of sprat spawning with peak spawning in May has remained relatively stable throughout the 1990s (STORE, 2001). Consequently, in the 1990s sprat spawned significantly earlier than cod, thus encountering different environmental conditions and reducing the temporal overlap with their predator in spawning areas. This may explain deviations in reproductive success of both species.

Available data on sexual maturity-at-age indicate significant interannual variability in proportions of sprat being sexually mature at age 1, which was earlier related to winter temperature (Elwertowski, 1960). Furthermore, the relative batch fecundity shows a significant intra- and interannual variability (Alekseeva *et al.*, 1997; STORE, 2001). An existing significant relationship between SSB and realized egg production can be improved by incorporating temperature in the intermediate water in May and growth anomaly through the preceding three-quarters of the year as a measure of the nutritional status of the adults (Köster *et al.*, 2002). Low winter temperature, reflected in low intermediate water temperature in May, may be responsible for changes in the nutritional condition and growth of sprat (e.g. Elwertowski, 1960) and by this reducing the individual egg production or may as well directly affect batch fecundity and numbers of batches spawned (Petrowa, 1960).

The decline in apparent growth rate of sprat appears to be related to a reduced food availability of calanoid copepods per individual sprat, mainly caused by a reduction in abundance of the largest copepod species *Pseudocalanus elongatus* (Möllmann *et al.*, 2003) and a concurrent increase in stock size of sprat. This limitation in food availability may have caused a decrease in individual egg production and potentially an increased age of attaining sexual maturation. However, given the high interannual variability in recruitment success in the second half of the 1990s, other variability generating processes appear to be of higher importance for the reproductive success.

Egg developmental success

In the Baltic, fish early life stage survival is known to be highly influenced by hydrographic conditions in the spawning areas (e.g. Bagge *et al.*, 1994; Grauman and Yula, 1989; Plikshs *et al.*, 1993; Parmanne *et al.*, 1994, Wieland *et al.*, 1994). The observation that live cod eggs are only encountered in water layers with oxygen concentrations $>2\,ml\,l^{-1}$ and temperatures $>1.5°C$, and that a salinity of 11 is necessary for successful fertilization, led to the definition of the so-called reproductive volume (RV), i.e. the water volume sustaining cod egg development (Plikshs *et al.*, 1993). Processes affecting the RV are: (i) the magnitude of inflows of saline oxygenated water from the western Baltic (MacKenzie *et al.*, 2000), (ii) temperature regimes in the western Baltic during winter, which affect the oxygen solubility prior to advection (Hinrichsen *et al.*, 2002b), (iii) river run-off (Hinrichsen *et al.*, 2002b) and (iv) oxygen consumption by biological processes (Hansson and Rudstam, 1990). Resolving the potential egg production by cod spatially showed that in some years a substantial fraction of the total annual egg production has been unsuccessful (in terms of recruit production), because eggs were exposed to extremely low oxygen concentrations in eastern spawning areas (Köster *et al.*, 2001b). This mismatch in egg production and suitable environmental conditions for egg development explains the drastic decline in reproductive success of cod from 1981 to 1985 despite high egg production.

Due to differences in egg specific gravity, egg development of cod and sprat occurs at different depths. Whereas cod eggs are neutrally buoyant at salinities of 12–17 (Nissling *et al.*, 1994), the range for sprat eggs is 7–13 (Grauman, 1965), i.e. the majority of sprat eggs occur shallower than cod. This implies that sprat egg survival is less affected by poor oxygen conditions than the survival of cod eggs. As sprat eggs occur at depths where the water temperature is affected by winter cooling (Wieland and Zuzarte, 1991), egg and larval development may be influenced by extreme water temperatures. In fact, weak year classes of Baltic sprat have been associated with severe winters accompanied by low water temperatures during peak spawning (e.g. Kalejs and Ojaveer, 1989; Grauman and Yula, 1989). A significant impact of temperature on egg developmental success has been found in the North Sea (Thompson *et al.*, 1981) and confirmed for the Baltic (Nissling, 2002), with temperatures below 4°C significantly reducing egg survival. As these temperatures occur regularly in the intermediate water layer, an effect on egg survival especially after severe winters is expected. In this respect, the absence of severe winters since 1986/1987 indicates favourable thermal conditions for sprat egg survival and most likely contributes to the generally high recruitment.

Egg predation

Substantial predation on cod eggs by clupeids has been described for the major spawning area of the Baltic cod stock, i.e. the Bornholm Basin. Egg predation is most intense at the beginning of the cod spawning season, with sprat being the major predator (Köster and Möllmann, 2000a). At this time spring spawning herring concentrate in their coastal spawning areas and do not contribute to the predation-induced egg mortality of cod. Sprat spawn in the Bornholm Basin from March to July, thus concentrating in cod spawning areas at times of high cod egg abundance. After cessation of spawning, the part of the sprat population leaves, resulting in a reduced predation pressure on cod eggs. With the return of the herring from the coastal areas to their feeding grounds in the Bornholm Basin, the predation on cod eggs by herring increases to considerable levels (Köster and Möllmann, 2000a).

The shift of cod peak spawning time from spring to summer (Wieland *et al.*, 2000) resulted in a decreasing predation pressure on cod eggs by sprat because of a reduced temporal overlap between predator and prey. Additionally, a decline in individual sprat predation on cod eggs was observed from 1993 to 1996, despite relatively high cod egg abundance in the plankton. This is partly explainable by a reduced vertical overlap between predator and prey. Owing to the increased salinity after the 1993 major Baltic inflow (Matthäus and Lass, 1995), cod eggs were floating in shallower water layers, while clupeids occurred deeper, because of enhanced oxygen concentration in the bottom water (Köster and Möllmann, 2000a) Thus, predation pressure on cod eggs appears to be higher in stagnation periods, characterized by the absence of inflows of oxygenated saline water from western neighbouring Baltic basins.

Egg cannibalism was found to be an important source of sprat egg mortality in the Bornholm Basin (Köster and Möllmann, 2000b), but appears to be less important in the more eastern areas. This has been explained by a more limited vertical overlap between predator and prey in these areas (STORE, 2001).

Larval development

Behaviour studies demonstrated that cod larvae exposed to oxygen concentration below 2 ml l^{-1} for 2 days were mostly inactive or moribund (Nissling, 1994) and that egg incubation at oxygen saturations of 40% or lower impacts on larval activity as well (Rohlf, 1999). Furthermore, Rohlf revealed that vertical migration into upper water layers does not start before day 4 after hatching. Hence, a significant impact on larval survival of the environment within and below the halocline can be expected. In an attempt to explain the variability of late cod egg production and larval abundance in the Bornholm Basin, Köster *et al.* (2001b) tested various environmental variables, i.e. the oxygen concentration in and below the halocline, temperature in the intermediate water, and wind-driven transport, for their explanatory power. However, these authors were unable to explain the major part of the variability in larval abundance. This led to the conclusion that either other factors influence the survival until the larval stage, or the variability in larval abundance (integrated over all developmental stages) is too high for a major impact of the tested factors to be detected.

For sprat, an impact of the temperature in the intermediate water on larval survival has been described by Köster *et al.* (2002). An increased larval abundance at above average spring temperatures has been explained earlier by the positive effect of higher temperature on the dynamics of the copepod *Temora longicornis*, which is the main prey species of sprat larvae (Grauman and Yula, 1989; Kalejs and Ojaveer, 1989). Consequently, warm winters since the late 1980s favoured sprat egg production and survival, as well as larval growth and survival.

The effect of food availability on growth and survival of cod larvae has been investigated using a coupled hydro/trophodynamic individual-based

model (IBM) (Hinrichsen *et al.*, 2002a). Model results suggest the necessity of co-occurrence of peak prey and larval abundances as well as favourable oceanographic conditions for high survival rates. The strong decline of the *Pseudocalanus elongatus* stock during the past two decades as a result of low salinities (Möllmann *et al.*, 2000) meant that early cod larvae changed from a non-food limited to a food limited state. If *P. elongatus* nauplii are present in the model, high survival rates occurred during spring and early summer, whereas omitting *P. elongatus* resulted in high mortality rates and only late hatched larvae survived (Hinrichsen *et al.*, 2002a). Thus, low *P. elongatus* availability may have contributed to the reduced recruitment of cod since the late 1980s.

Also, sprat larvae may face food limitations; however, they usually drift out of the spawning areas more rapidly than cod larvae due to their residing in shallower depths (e.g. Wieland and Zuzarte, 1991). Thus, rapid drift to coastal water areas with higher abundance of *Acartia* spp. and *Temora longicornis* nauplii being their preferred food items (Voss and Köster, 2002) appears to be the normal case.

Predation on juveniles

Juvenile cod suffer from cannibalism (Sparholt, 1994; Neuenfeldt and Köster, 2000). As in other cod stocks, the intensity of cannibalism is related to predator abundance, but also to the juvenile concentrations, which depend upon the habitat volume occupied and the overall abundance of cod (Anderson and Gregory, 2000). Apart from medium- to long-term distribution changes, interannual variability in cannibalism may be influenced by changing hydrographic conditions as well (Uzars and Plikshs, 2000). For example, low oxygen concentration in the deep Baltic basins may force the adults into shallower slope areas and low temperature in shallow waters may force juveniles into deeper water, by this increasing the spatial overlap between predator and prey and hence cannibalism. This suggests that the process is most pronounced in stagnation periods, especially after cold winters.

Predation on 0-group sprat by cod occurs regularly, although predation mortality rates from MSVPA are significantly lower than for 1-group sprat. The intensity of the predation is most likely modulated also by hydrographic conditions and by species-specific preferences and tolerance levels to hydrographic variables, resulting in variable potential predator/prey encounter volumes (Neuenfeldt, 2002).

Regime shift from a cod-dominated to a sprat-dominated system

As seen from the results of the MSVPA, the upper trophic levels of the Central Baltic changed during the past 20 years from a cod- to a sprat-dominated system (Figure 7). The decline of the cod stock was caused by a continued high fishing pressure and a concurrent recruitment failure, which according to our review was mainly driven by: (i) anoxic conditions in deep water layers of spawning sites causing high egg mortalities, (ii) high egg predation by clupeid predators, (iii) reduced larval survival due to the decrease in abundance of the main food

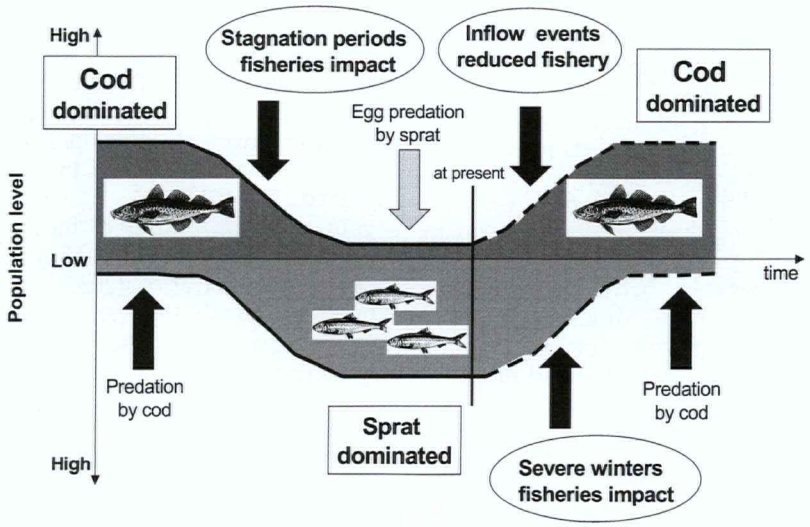

Figure 7. Schematic presentation of processes stabilizing a cod-dominated or sprat-dominated system in the Central Baltic. Note the vertical line represents the situation in the 2nd half of the 1990s with the regime shift taking place in late 1980s and early 1990s.

item *P. elongatus*, and (iv) high juvenile cannibalism at high stock density. The intensity and significance of all these processes are in one way or the other steered by the hydrographic conditions, which in the 1990s were characterized by low salinity due to a lack of inflow of highly saline water from the North Sea, Skagerrak, and Kattegat, as well as increased river run-off, but also by warmer thermal conditions. An increasing fishing pressure accelerated the decline of the cod stock, with current exploitation levels being still on a very high level. The decline of the cod stock released sprat from predation pressure, which in combination with high reproductive success, due to in general favourable temperature conditions enhancing egg and larval survival, resulted in exceptionally high sprat stock sizes in the 1990s. Indications for compensatory processes in growth, maturation, and individual egg production exist for both species; however, they appear to have limited impact on their stock dynamics.

As a result of these processes, the dominance of one or either predator may stabilize a cod-dominated or a sprat-dominated system. Destabilization of the sprat-dominated system may be caused either by unfavourable hydrographic conditions for reproduction, e.g. low water temperatures in spring following severe winters and subsequent recruitment failures of sprat, or high mortalities caused by the fishery, with concurrent low fishing pressure on cod and the presence of inflow events into the deep Baltic basins.

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